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Vertebrate Predator Control: Effects on Prey Populations in Terrestrial and Aquatic Ecosystems

Contrôle des prédateurs vertébrés : effets sur les populations de proies dans les écosystèmes terrestres et aquatiques

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ABSTRACT

Ecologists have known for some time that predators can have significant effects on terrestrial and aquatic prey populations. Culling is widely practiced as a means to limit predation on livestock and game. Changes in species' distributions and abundance illustrate that culling programs can be very effective at reducing predator density. Culling has also been used to reduce marine mammal populations in many parts of the world. Coastal pinniped species have usually been the target of such programs, but dolphins and large cetaceans have also been culled. The extent of marine mammal population reduction and the response of targeted prey populations to culls have rarely been evaluated.

There are several conclusions that can be drawn from experimental studies in terrestrial systems and more model-based approaches in aquatic systems. First, predator removal can increase productivity and population size of target prey populations, but not always. Second, these studies typically have involved large proportional reduction (>50%) in predator populations, presumably to increase effect size and the statistical power to detect a significant effect. Third, the effects of culling are typically dependent on continued control, and in the absence of control the benefits rapidly disappear. This underscores the need for predator removal to be a long-term management strategy. Fourth, at least in the case of marine mammals, few studies have clearly articulated measurable objectives for prey population recovery or increase and most have not evaluated the success of the control program with respect to those objectives. Fifth, culling predators often has non-intuitive and unintended consequences for both target and other predator and prey species. Despite their prevalence, the effectiveness, efficiency and the benefit: cost ratio of culling, programs have been poorly studied.

RÉSUMÉ

Les écologistes savent depuis longtemps que les prédateurs peuvent avoir des impacts importants sur les populations de proies terrestres et aquatiques. L'abattage est communément pratiqué comme moyen de limiter la prédation sur le bétail et le gibier. Les changements de distribution et d'abondance des espèces montrent que ces programmes d'abattage peuvent être très efficaces pour réduire la densité des prédateurs. Ils ont aussi été utilisés afin de réduire certaines populations de mammifères marins dans différents endroits du monde. Les espèces côtières de pinnipèdes ont généralement été la cible de tels programmes, mais les dauphins et les grands cétacés ont aussi été l'objet d'abattages. L'importance de la réduction des populations de mammifères marins et la réponse des populations de proies à ces abattages ont rarement été évaluées.

Plusieurs conclusions peuvent être tirées des études expérimentales réalisées sur les systèmes terrestres ainsi que des approches de modélisation pour les systèmes aquatiques. Premièrement, la suppression de prédateurs peut augmenter la productivité et la taille des populations de proies ciblées, mais ce n'est pas toujours le cas. Deuxièmement, ces études impliquent habituellement la réduction d'une grande proportion (> 50 %) des populations de prédateurs, probablement pour augmenter l'importance de l'effet et l'efficacité statistique afin de détecter un effet significatif. Troisièmement, les effets des abattages reposent habituellement sur un suivi continu et, en l'absence de contrôle, les bénéfices disparaissent rapidement. Ceci souligne à quel point il est important que la suppression de prédateurs constitue une stratégie de gestion à long terme. Quatrièmement, du moins dans le cas des mammifères marins, peu d'études ont exprimé clairement des objectifs mesurables quant au rétablissement et à l'augmentation des populations de proies et ont évalué le succès du programme de contrôle par rapport à ces objectifs. Cinquièmement, l'abattage de prédateurs a souvent des conséquences contre-intuitives et non désirées, tant sur les espèces ciblées que sur d'autres espèces de proies et de prédateurs. Malgré la prévalence de ces programmes, leur efficacité, leur efficience et le rapport entre les bénéfices et les coûts ont été peu étudiés.

INTRODUCTION

Some 270 species comprise the Carnivora, a diverse group of terrestrial and aquatic species representing 11 families of mammals. Many of these species limit or regulate prey species populations and their top-down effects alter the structure and functioning of ecosystems, either through control of herbivore populations or of mid-sized predators when predation pressure from top predator is reduced (Berger et al. 2001; Crooks and Soule 1999; Johnson et al. 2007; Terborgh et al. 1999; Terborgh et al. 2001). Because of these effects and the prey species eaten (i.e., often commercially valuable) carnivore-human conflicts are common and widespread (Treves and Karanth 2003). Although these conflicts have a long history (wolf control to protect livestock dates back 2500 years in Greece, Reynolds and Tapper 1996), expansion of humans activities combined with the recovery of over-exploited wildlife populations has led to an increase in contact and conflict between people and wildlife predators in many parts of the world (Berger 2006; Woodroffe and MacDonald 1995). Livestock depredation is the most common source of conflict involving a wide range of predators (Graham et al. 2005; Baker et al. 2008), but predation by raptors on game birds is an increasing source of conflict (Valkama et al. 2005). In aquatic systems, predation by marine mammals on fish and shellfish species of commercial importance or damage to fishing gear has been a source of conflict with fisheries for over a century (e.g., Merriam 1901; Worthington 1964; Fiscus 1979; Gulland 1987) and likely much longer. Predators also come into conflict with humans through the transmission of diseases and parasites (Baker et al. 2008; Malouf 1986).

Many terrestrial and aquatic ecosystems have been severely changed by commercial exploitation of living resources, habitat destruction, and the effects of invasive species (Jackson et al. 2001; Lotze and Worm 2009). A common consequence of those modifications is that some species become much less abundant, to the point of being considered threatened or endangered, and others become much more abundant. Where one of the threats to a threatened or endangered species is predation, the question arises as to whether to control the predator population to reverse the decline in the prey population or to remove anthropogenic threats and hope that natural processes to return the ecosystem towards a more desirable state. In both cases, the goal is to return the ecosystem to a state that will deliver the desired ecosystems serves, such as increased exploitable fish biomass. The merits of each of these management approaches and the likelihood that they will achieve stated goals continue to be debated.

Implicit in the "let nature do it" approach of no intervention is that if left alone the system will return to some former more desirable state. However, there is considerable evidence that ecosystems do not generally have a single characteristic state (Scheffer et al. 2001) and therefore we may be misguided in thinking that passive management actions will be enough (Lessard et al. 2005). There may be cases where ecosystem management may require active food-web manipulation when simple protection from further human threats appears likely to fail. This underscores the need to determine the sources of mortality of the target species and assess the likelihood that simple protection would be insufficient (Lessard et al. 2005).

Experimental studies of streams, lakes, and coastal marine ecosystems have shown that changes to predator populations can have cascading effects on prey populations (Carpenter et al. 1995; Mazumder et al. 1990; Estes et al. 1998; Jackson et al. 2001). However, it is not clear how the conclusions of those studies can be applied to continental shelf ecosystems (Worm and Myers 2003). Not only are such systems considerably larger, but there is debate about the importance of top-down forcing in marine ecosystems compared to bottom-up forcing of environmental variability (e.g., Strong 1992; Verity and Smetacek 1996). So the challenge is to

determine if the patterns found in better studied terrestrial and fresh water ecosystems can be generalized to continental shelf and oceanic systems.

The objective of this review is threefold. The first is to briefly review predation theory in the context of predator effects on prey populations and the second is to evaluate the efficacy of vertebrate predator control (i.e., culling – killing animals to reduce the perceived negative effects of a predator on prey species of interest to humans) on prey population dynamics. We review both terrestrial and aquatic examples, with a focus on control programs of marine mammals. In most cases, this amounts to determining if experimental removal or culling predators increased the productivity and population size of the target prey species. Although the focus of the review is on the effectiveness of culling as a management tool, some commercial harvests appear to have the dual objectives of deriving products from the predator and culling (i.e., killing of predators to meet an objective with respect to a prey species). Finally, we attempt to draw some lesson from what has been learned about the efficacy of predator control as a management tool.

METHODS

We reviewed the literature by querying the Web of Science for articles containing the following topic expressions during the period 1900- 2010: vertebrate "predator control", vertebrate "predator removal", "predator-human conflict", "predator-prey conflict", "shark control", "shark fishery impacts", "seal-fishery", cull*, culling, and "seal predation". We focussed on studies in which carnivorous mammals, birds, or large predatory fishes were removed with the objective of increasing the abundance of targeted native prey species.

We excluded papers dealing with the indirect effect of predators on plants and herbivore-plant interactions. Also excluded were studies were the objective of the control program was to prevent or reduce the spread of disease by the predator, studies focussing on the effects of poison bait on non-target species, and most studies involving introduced species and livestock. Livestock losses to carnivores and the factors influencing those losses and culling program to alleviate livestock losses have been previously reviewed (Baker et al. 2008). Because culling has been so extensively practiced to reduce livestock losses to predators, some livestock studies are included as they illustrated some important consequences of culling. Introduced species lack co-evolved responses of predator and prey to one another and therefore they may not be representative of predator-prey interactions between species with a long evolutionary history. There is good evidence that introductions of invasive species can have dramatic and widespread consequences for communities (e.g., Zaret and Paine ; Kitchell and Crowder 1986; Croll et al. 2005). Sinclair et al. 1998) cite a number of studies documenting the decline or extinction of native prey species by introduced predators.

PREDATOR-PREY INTERACTIONS BACKGROUND

Many consider it obvious that removing predators should increase prey populations, but predator-prey interactions are far too complex to assume this. For example, if prey are limited by habitat then removal of predators may do little good. Predator control is based on the assumption that predators limit prey abundance and that a decrease in predators will increase prey productivity or abundance, or at least reduce the overall losses of prey. The success of predator removal depends on what fraction of natural mortality is caused by the predator and how other sources of natural mortality interact. Thus, to successfully manage predator and prey populations, in order to reduce conflicts between stakeholders, it is important to know if there is

indeed an impact of vertebrate predators on prey, and then to quantify this impact (Graham et al. 2005).

The view that predators can limit prey populations has been a source of debate dating back to the middle of the last century (Nicholson 1933; Andrewortha and Birch 1954). Population limitation occurs when factors, such as predation, reduce the rate of population growth to limit the population below its carry capacity (Sinclair and Pech 1996). Some ecologist held the view that predators had little effect on prey populations as they killed only those individuals that would have died of other causes. This "compensatory hypothesis" states that predators consume the proportion of the prey population that would have suffered natural mortality in the absence of predation (Errington 1946). This hypothesis was supported by early work on red grouse (*Lagopus lagopus scoticus*) population dynamics (Jenkins et al. 1963), and reinforced by evolutionary arguments that co-evolved predator and prey systems implied that prey populations were able to cope with native predators (Reynolds and Tapper 1996). Under this hypothesis, control of predators would not be expected to result in larger or more productive prey populations. More recent studies have found support for the "additive hypothesis" which states that predation causes mortality above the level that would have occurred in the absence of predation and thus can limit prey population numbers (see Valkama et al. 2005). Under this hypothesis, predator removal can be expected to result in either increased productivity or abundance of prey.

Both responses to predation have been documented in wild populations (e.g., references in Holt et al. 2008), and there is almost certainly a continuum of responses with the compensatory mortality hypothesis at one end of the continuum and the additive mortality hypothesis at the other. Sinclair and Pech (1996) argued that completely additive mortality and exact compensation are unlikely conditions, and that where resources are density-dependent, other non-density dependent sources of mortality will always result in a reduced equilibrium population.

Predators can exert density-dependent, inverse density-dependent, and more complex effects on prey (Sinclair and Pech 1996). Total response of predators to changes in prey density is the product of two components – the functional and numerical response, and these represent the total proportional mortality imposed by the predator on its prey. At high prey density both functional and numerical responses reach an asymptote because of handling time and satiation in the former and interference in the latter. This means the prey will experience decreasing proportional mortality, i.e., predation is dispensatory at high prey density.

The functional response of a predator can be classified as prey dependent, when prey density alone determines consumption rate, predator dependent, when both predator and prey numbers affect the response and multi-species dependent, when species other than the focal predator and its prey influence the response (Abrams and Ginzburg 2000). The ratio-dependent functional response has been argued to be a better approach for modelling predation (Arditi and Ginzburg 1989). This is a type of predator dependence in which only the ratio of predator to prey population size and not absolute numbers determines predation rate.

Abrams and Ginzburg (2000) made four predictions about the nature of functional responses. First, that prey dependence and ratio dependence should both be rare because at high predator density predators are likely to interfere with one another and at low predator density, their rarity will prevent the capture of large numbers of prey even though the model predicts it. Second, predator dependence will be common such that both predator and prey density will influence the response. Third, responses will often be affected by species other than predator and prey. For example, changes in food density changes the risk-taking of foragers and this can be expected

to affect the functional response of predators to prey. Finally, predator dependence of the numerical response will be common because other variables affect the numerical response, such as competition over resources other than prey.

Effects of predators on prey populations also depend on the nature of the functional response. If the predator functional response is Type II, the proportional mortality on prey is dispensatory at all prey densities. If the functional response is Type III, then the accelerating part of the curve at low prey density will have a density dependent effect on prey, whereas the decelerating part at high prey density will be depensatory. If prey density is low and the predation rate is greater then recruitment, predators can drive prey extinct. For this to happen, predators must have a Type II functional response, no density dependence in numerical response, and predators must depend primarily on another prey. Examples of this are reported for wolves (*Canis lupus*) driving caribou (*Rangifer tarandus*) extinct while depending on moose (*Alces alces*) (Seip 1992) and small carnivores drive passerine bird populations extinct (Terborgh 1992). This situation would appear relevant to the interaction between grey seals (*Halichoerus grypus*) and Atlantic cod (*Gadus morhua*) as cod may forms a relatively small fraction of the overall diet. However, we can expect a delay in the response of seals to changes in cod densities, which could lead to a limit cycle where predation oscillates between high and low predation rates.

CULLING PREDATORS

Terrestrial Systems

Game and avian species are often taken by mammalian carnivores and raptors. Globally, predator culling has been and continues to be the most commonly used tool for increasing game abundance for hunters (Cote and Sutherland 1997; Reynolds and Tapper 1996). Culling can be done proactively, whereby animals are killed in anticipation of risk to prey, or reactively, whereby the goal is to selectively remove predators that are actually causing damage (Baker et al. 2008). The former usually involves the killing of larger numbers of animals than the latter which is intended to be highly selective. Despite the widespread use of culling to manage carnivore populations with respect to food production, there is rather limited scientific evidence that such management is generally effective in increasing livestock production over the longer term and few studies have attempted to evaluate the success of culling in economic terms (Baker et al. 2008). The American National Research Council made the same observation with respect to wolf and bear management to enhance ungulate populations in Alaska (Anonymous 1997).

Predator control of terrestrial vertebrates has been used in the UK for over 200 years, providing extensive data from which to make inferences about the success of such programs (Reynolds and Tapper 1996). Holt et al. (2008) used 40 published studies in a meta-analysis to quantify the effects of predators on the abundance of their prey. They found that predator removal caused a 1.6 fold increase in the abundance of prey. However, they also found significant heterogeneity in the prey response to culling with positive cases involving mammalian or multiple predators, but they found no significant effect of bird predation. The authors considered that this taxon effect may have reflected the difference in effects of native (all avian in the UK data) and non-native predators (all mammals in the UK data). They further suggested that prey populations may suffer compensatory mortality when preyed upon by native predators, in multiple predator communities, but additive mortality may be more common with non-native predators.

Several meta-analytic studies have been used to evaluate the effectiveness of predator removal to enhance bird populations. Coté and Sutherland (1997) found that predator control was generally effective in increasing hatching success and post-breeding population size, but not reliably effective (no significant overall effect) in increasing the breeding population. These authors also noted that based on limited evidence from mainland studies, predator removal did not have long-lasting effects, and, if not maintained the benefits rapidly disappeared. A recent study updated the work of Coté and Sutherland (1997) and summarized the results of 83 predator removal studies from six continents to conserve vulnerable bird populations (Smith et al. 2010). Most of the studies analyzed (63%) compared predator removal areas with control areas and the remainder measured the responses of bird populations before and after predator removal. The meta-analysis indicated predator control increased hatching success and fledging success, but did not have a significant positive effect on post-breeding population size, even though there was a positive longer-term increase in breeding population numbers. They also found significant heterogeneity in the population response to predator removal, although in these studies whether the predator was native or introduced did not explain any of the heterogeneity. Despite these findings, it has been shown that introduced predators generally have double the impact of native species (Salo et al. 2007). Smith et al. (2010) also found that larger increases in bird populations were achieved by culling all predators rather than a subset, as removing all predators excluded meso-predator release. The effects of removals on predator densities could not be evaluated as most studies did not present this type of information. Finally, as previously concluded, the authors (e.g., Coté and Sutherland, 1997; Tapper et al. 1982) noted that if predator removal is not continued, any positive effects on prey populations soon disappear. This underscores the need for predator removal to be a long-term management strategy.

Large-scale experimental predator removal studies also have been used to understand the effects of predators on the dynamics of native prey populations. Cyclic fluctuations of many northern mammal populations are well known and the mechanisms underlying those fluctuations have generated considerable interest from ecologists. One of the better studied systems is the 10-year cycle of snowshoe hare populations and those of their mammalian and avian predators. Over a 7-year period, Krebs and Sinclair and their colleagues undertook a series of manipulative experiments using a factorial design to tease apart the effects of food and predation on snowshoe hares (*Lepus americanus*) (Krebs et al. 1995; Sinclair et al. 2000). Predator removal had little effect on hare density during the peak years, but became pronounced late in the decline and low phase of the hare cycle. Averaged over the peak and decline phase, predator removal doubled hare density, but the combined effect of predator removal and food supplementation increased hare density 11-fold suggesting that food had a much greater effect on prey density than predation.

Another interaction that has been well studied is bear predation of ungulates, particularly of young animals. The perception that bears are effective predators of ungulates has lead to reduction programs in both Canada and United States (Zager and Beecham 2006). Black bear (*Ursus americanus*) predation on a low-density elk (*Cervus canadensis*) population appeared to be additive as survival and recruitment increased in the two years following bear removal, but then declined to pre-removal levels two years later. Similar changes in elk recruitment and survival were seen in neighbouring areas where bears were not removed (Schlegel 1986), suggesting that factors other than bear predation were more important. Other studies have shown significant increases in ungulate offspring-cow ratios after bear reduction, and that bear mortality was increasingly additive as moose density declined (Ballard 1992; Gasaway et al. 1992). Thus, the impact of bear predation appears to differ in low versus high density ungulate populations (Gasaway et al. 1992). At low density, evidence indicates that bears can limit moose densities for an extended period of time, suggesting that predation is depensatory and

that the prey is being held in a predator pit. By contrast, at high density, bear mortality appears to become increasingly compensatory (McCullough 1984). Overall, bear removal studies indicate a short- but not long-term increase in ungulate calf survival. However, these studies often provide little understanding of the factors that may predispose calves to predation, or to other sources of mortality (Zager and Beecham 2006). In contrast to calves, adult female survival remains high regardless of the dominant natural mortality factors (Gaillard et al. 1998).

Wolf predation has also been extensively studied and there is good evidence that wolf predation limits the size of moose and caribou populations in Alaska and the Yukon (Hayes et al. 2003). However, less is known about whether wolf predation is additive or compensatory in relation to other sources of mortality. Hayes et al. (2003) conducted a series of large scale, manipulative experiments over five years to test the hypothesis that wolf predation limits the size of caribou, moose and Dall sheep (*Ovis dalli*) populations in the Yukon. Unlike many other studies, the design of the experiment included an evaluation of other factors that might affect recruitment and survival so that the effect of wolf reduction could be assessed after accounting for the influence of other factors. Over the 5-yr period, wolf population reduction ranged from 69-83% and both moose and caribou populations increased compared to controls. However, there was no response to wolf removal in the case of Dall sheep, providing evidence that wolf predation was not limiting sheep numbers. Although predictions about the impact of wolves on moose and caribou were generally supported, the authors found different levels of support for predictions about changes in recruitment, adult survival, and population trends for the three species, underscoring the incomplete nature of our understanding of predator-prey dynamics. These controlled experiments also showed that predation by wolves was largely additive (77%) for the low to moderate densities of both moose and caribou studied (Hayes et al. 2000). About 25% of predation events were considered compensatory as they involved old animals that would have died had they not been killed by wolves. These results agree with the conclusion that wolf predation on ungulates is usually additive when prey densities are below the resources limitations (i.e., carrying capacity) (Theberge 1990; Gasaway et al. 1992). Wolf kill rate was proportional to pack size and not to prey density, indicating the lack of a functional response at least over the range of prey densities studied. Wolf predation was also unrelated to the number of calves available or the ratio of moose to caribou.

From the review of studies of wolf predation on ungulates, Theberge and Gauthier (1985) developed verbal models for the conditions under which predator control should have a positive effect on wolf-ungulate interactions. Of the 18 studies reviewed by the authors, 13 concluded that wolves were limiting their ungulate prey. Nevertheless, Theberge and Gauthier argued that the response of an ungulate population to a reduction in wolf numbers should depend strongly on how close the ungulate population is to a resource ceiling. If close, then any gains from the release of predation by wolves may be lost through starvation and the two sources of mortality would be compensatory.

One of the better studied predator-prey conflicts with people concerns hen harrier (*Circus cyaneus*) predation on red grouse in the UK (reviewed in Thirgood and Redpath 2008). This is a conflict between hen harrier conservation and grouse management for the purpose of sport hunting. Management of grouse involves burning heather on the moorlands, controlling predators and parasites and is recognized as providing ecological, social and economic benefits. Hen harriers are protected, but illegal killing of harriers is the principle factor limiting their population growth (Sim et al. 2007). Harriers are killed because hunters believe they reduce grouse harvests. Ecological evidence supports this hypothesis (Thirgood et al. 2000) with high harrier densities limiting grouse populations resulting in reduced harvests and eventual closure (Redpath and Thirgood 1997). Several approaches to reduce this conflict have been proposed (Table 1) and several stakeholder forums have attempted to address the

conflict. After years of planning, an attempt to restore grouse populations through manipulation of habitat, predator removal, and diversionary feeding was begun in 2008 in the Langholm Moor. Nevertheless, illegal killing of harriers is widespread and thought to be responsible for the continued decline of harriers in areas of grouse shooting (Sim et al. 2007).

Given that the science of this predator-prey interaction is reasonably well understood and the considerable stakeholder interest, it is reasonable to ask why mitigation of this conflict has been so difficult to achieve? Three reasons have been proposed (Thirgood and Redpath 2008). The first is the entrenched positions of the major stakeholders on both sides. Second, a certain acceptance of the status quo, harriers continue to be shot by hunters and conservationists continue to demand changes, and third, a lack of money. Research needed to evaluate the effectiveness of mitigation is field-based and expensive. The Langholm Moor Demonstration Project will cost more than £ 3 million over 10 years and will use much of the funds that might be available to evaluate other approaches.

Changes in breeding success and abundance of other ground-nesting birds in response to an 8-year-field experiment of predator removal in north England have recently been reported (Fletcher et al. 2010). Reduction in the abundance of red fox (*Vulpes vulpes*) (-43%) and carrion crow (*Corvus corone*) (-78%) populations, the most abundant predators, led to threefold increases in breeding success of all five species studied and smaller increases in breeding numbers (approximately 14%/year) of four of seven species studied.

Aquatic Systems

Double-crested cormorants (*Phalacrocorax auritus*) have increased in much of North America and growing numbers of birds have fuelled concern about impacts on fish populations. Studies on the consumption of fish suggest that these piscivorous birds can affect fish stocks depending on bird densities and the availability of alternative prey (references in Derby and Lovvorn 1997). Cormorant populations expanded across the Great Lakes between the 1900s and 1950s (OMNR 2006). Early control measures of destroying eggs and nests were ineffective and did not significantly reduce the Great Lakes population. A cormorant control program remained in effect in Ontario until 1966. Throughout the 1960s and early 1970s cormorant populations experienced a dramatic decline due to eggshell thinning and by the early 1970s the Great Lakes-wide population was approximately 130 nesting pairs with no breeding birds remaining in the U.S. portion of the Great Lakes. From 1973 to 1993, cormorant numbers increased by nearly 300-fold to 38,000 nesting pairs and 80 new colonies across the Great Lakes and by 2005 this number had increased to 113,000 pairs. Recently, numbers in Lake Huron and Ontario, the largest populations, appear to be stabilizing (OMNR 2006).

This dramatic increase in cormorant abundance has fuelled debate about the effects on recreational and commercial fisheries and vegetation. Control measures in Presqu'ile Provincial Park, Ontario, were effective in reducing the number of nests from about 12,000 in 2002 to 4,600 in 2005. Elsewhere in Canada, from 1989 to 1994, Quebec undertook a cormorant management program in the St. Lawrence estuary to reduce the breeding population from approximately 17,000 nests to 10,000 nests in order to protect the biodiversity of island vegetation in the area (Bedard et al. 1995). During the five-year program approximately 8,000 cormorants were culled and 26,000 nests were oiled. Overall, the control program reduced the cormorant population and was effective in reducing vegetation damage in the area. However, since 1994 cormorants on the St. Lawrence estuary have rebounded.

Due to growing conflicts with the double-crested cormorants in the United States, in November 1999 the U.S. Fish and Wildlife Service, in cooperation with other government agencies,

prepared an Environmental Impact Statement and National Management Plan for the double-crested cormorant to address these conflicts (USFWS 2003). In 2003, after considerable public consultation, the final management plan was released with the goal "to reduce local resource conflicts, increase management flexibility, and conserve a healthy cormorant population over the long term". The Order was applicable to 24 mid-continental states and allowed management agencies and federally recognized Tribes to control double-crested cormorants without a depredation permit when necessary. During the summer of 2004, several states initiated control programs after issuance of a depredation order including Arkansas (193 birds killed and 95 nests destroyed), Michigan (1 424 birds killed and 3 114 nests oiled), New York (482 birds killed, 2 818 nests destroyed, and 11 450 nests oiled) and Vermont (208 birds killed and 1 458 nests oiled) (USFWS 2003; Hanisch and Schmidt 2006). The order remained in effect until April 30, 2009.

Of the 24 applicable States, Michigan and New York had the most intensive management programs and appeared to be effective in reducing cormorant numbers and their associated impacts on fisheries, vegetation, and other wildlife (Farquhar et al. 2004; USFWS 2003). In 2000, the yellow perch (*Perca flavescens*) fishery of the Les Cheneaux Islands region of Lake Huron, Michigan, a recreational fishery since the start of the twentieth century, experienced an unprecedented collapse (Fielder 2010). Research based on data from 1969 to 2004 showed that trends in the abundance of double-crested cormorants had the greatest explanatory power for five key population variables of yellow perch including the annual mortality rate (Fielder 2008). The study concluded that the abundance of cormorants were one of the contributing factors to the decline of yellow perch. A control program was implemented in 2004, under authority of the United States Fish and Wildlife Service Public Resource Depredation Order in the Les Cheneaux Islands region that involved annual egg oiling and the culling of adults with the aim of reducing the number of cormorants and subsequently predation on yellow perch. Alongside the management program, the success of the effort was evaluated through monitoring studies on the status of cormorant and yellow perch populations. The study found the relationship between the number of breeding cormorants and the level of foraging activity in the Les Cheneaux Islands region was more complex than expected. Although the number of breeding cormorants in the region declined by 74%, the decline in foraging activity was not of the same magnitude (Dorr et al. 2010). During the management period, significantly more cormorants used the Les Cheneaux Islands region compared with surrounding regions, and the level of foraging activity declined significantly in all regions except in that of the Les Cheneaux Islands. Nevertheless, cormorant numbers had declined compared with numbers in 1995; due in part to an earlier introduction of raccoons, and flock size was smaller and more dispersed. Overall the management program was successful since the decline in abundance of cormorants and more dispersed foraging improved the status of the yellow perch population through increased abundance, lower mortality, improved recreational catch rate, an increase in the mean age and an increase in recruitment and longevity of year classes (Dorr et al. 2010; Fielder 2010).

Cormorant predation has also been implicated in the status of smallmouth bass (*Micropterus dolomieui*) fishery in Lake Ontario, New York. Although there was "...a strongly held public perception that smallmouth bass fishing was poor and double-crested cormorant predation was excessive", the evidence to directly link double-crested cormorants to the decline in the fishery was insufficient and other environmental changes that took place during the same period added a layer of uncertainty as to the cause of the decline (Schnieder et al. 1999). In response, the New York State Department of Environmental Conservation and the United States Geological Survey conducted an intensive field study to determine the impact of double-crested cormorants on smallmouth bass and other fisheries in the eastern basin of Lake Ontario (Schnieder et al. 1999). Overall, the results from the numerous studies concluded that predation by double-

crested cormorants on smallmouth bass was excessive. Subsequently, a management plan and further research was developed and implemented to improve the smallmouth bass fishery and reduce the number of breeding cormorants. After a five-year period, it was concluded that the management plan, alongside research on cormorants, was successful in reducing the numbers of cormorants and their predation on fish species, and studies had confirmed the link between cormorant abundance and predation on smallmouth bass and yellow perch (Burnett et al. 2002; Farquhar et al. 2004; Lantry et al. 2002). The program was continued under the new Depredation Order and since 2003 the abundance of cormorants and their predation on warm-water fish in Lake Ontario has continued to decline (Johnson et al. 2010).

Predator–prey dynamics within some seabird communities have been altered owing to the negative effects of fisheries on prey populations and by the increase of alternative food supplies, such as fishery discards, which subsidize predators (Votier et al. 2004). Over the last century gull populations have increased substantially (Duhem et al. 2008) and large gulls are perceived as a pest by wildlife managers for a large number of reasons, including their impact on smaller and threatened synoptic species (Feare 1991; Vidal et al. 1998; Finney et al. 2003; though see Oro and Martínez-Abraín 2007). Conservation agencies have set up culling programs to control gull populations, which typically consist of systematic removal of large numbers of eggs, chicks or breeding adults (e.g. Blokpoel and Spaans 1991). Culls are usually conducted on the assumption that all birds are equally likely to impact threatened species, but there is increasing evidence that this may not be the case in a variety of taxa (fish – Svanbäck and Persson 2004; mammals – Estes et al. 2003 et al., 2003; birds – Guillemette Guillemette and Brousseau 2001; Martínez-Abraín et al. 2003; Oro et al. 2005).

Yellow-legged gulls (*Larus michahellis*) prey upon both breeding and immature storm-petrels (*Oceanites oceanicus*) and the resulting mortality is additive to other causes of mortality (Walmsley 1986; Zotier et al. 1992; Borg et al. 1995; Adam and Booth 2001; Oro et al. 2005). The effects of a selective culling of this top seabird predator on the survival, reproductive success and predatory pressure of a secondary prey have been evaluated (Sanz-Aguilar et al. 2009). Survival was estimated from mark-recapture data for a period before culling (1993-2003) and during culling (2004-2007). Overall, removal of only six gulls and 10 additional individuals nesting in the proximity of petrels led to a mean reduction of 65% in the number of petrels found in gull pellets. Experimental results showed that predation by gulls affected negatively both adult annual survival probability and breeding success of petrels, and after removing specialist gulls, adult survival probabilities and breeding success of storm-petrels greatly and rapidly increased (16% and 23%, respectively). There was no follow up so that it is not possible to determine how long the benefit of culling persisted.

Marine Mammal Culls

Culling marine mammals ostensibly to protect fish stocks has a long history dating back perhaps more than a century (Lavigne 2003). For example, in 1899, the California State Board of Fish Commissioners authorized a two-year cull of California sea lions (*Zalophus californianus*) on the grounds that sea lions were "highly destructive of the salmon fishery" (Merriam 1901). However, analysis of sea lion stomach contents failed to substantiate this, but the cull went ahead anyway. Complaints about the effects of seals on fisheries in the United Kingdom are thought to have begun in the 1920s, in connection with damage done to salmon by grey seals (Rae 1960). The perceived conflict between harvesters and marine mammals has recently been further manifested in the calls for increased whaling in the context of ecosystem management and the "whales-eat-fish" argument (Gerber et al. 2009). In all cases these conflicts are about perceived economic loss and the belief that the consumption by marine mammals represents biomass that would otherwise be available to fisheries.

The long history of culling marine mammals, usually pinnipeds, has involved multiple species and been conducted in different parts of the globe (Table 2). Grey, harbour (*Phoca vitulina)*, and ringed (*Histriophoca fasciata*) seals have been the main targets of control of phocid species. These species have coastal distributions making them accessible to hunters. Similarly just three otariid species, Steller (*Eumetopias jubatus*) and California sea lions and Cape fur seals (*Arctocephalus pusillus pusillus*), seem to have been the main target of control and again they have coastal distributions during summer. Common features of marine mammal culls to date are the lack of explicit and measurable objectives with respect to target populations and usually with respect to the reduction in the size of the marine mammal population to be achieved, other than that there be many fewer of them.

Pinnipeds

One of the first active control programs concerning a marine mammal (mainly ringed and grey) was undertaken in the Baltic Sea (Table 2). As the 19th century ended, seals gradually lost their economic value, and instead became regarded as competitors with fishermen. Several bounty systems were introduced to reduce the seal stocks and bounties were paid during the periods 1889-1927 and 1941-1977 in Denmark, 1903-1967 in Sweden and 1909-1918 and 1924-1975 in Finland (Harding and Harkonen 1999). Bounties dramatically reduced the population by perhaps 80% by the 1950s. This decrease was followed by a second decline in the 1960s in numbers because of reduced reproductive success caused by pollutants (Harding and Harkonen 1999).

Similarly, from about 1887 onward, sea lions and harbour seals were considered to be in conflict with fisheries from Alaska to California and control programs were undertaken to limit their populations (Table 2). One of the longest periods of culling took place in British Columbia, this despite the fact that the harbour seal population had been decimated by a long period of commercial harvesting that ended in 1914 (Olesiuk 2009). An average of more than 2900 harbour seals were reported killed each year for bounty in most years between 1914 and 1963 (Bigg 1969). However, at least this many likely went unreported (Bigg 1969). The cull was effective in holding the population roughly stable, at perhaps 40% of historical abundance, until another period of commercial harvesting dramatically reduced the population to about 10% of estimated historical population size (Olesiuk 2009). In 1970 the population was protected. Steller sea lion numbers were also controlled along the British Columbia coast up until their protection in 1970. Based on historic records of kills and counts, and estimates of trends in abundance through 1982, it was concluded that the control programs and commercial harvests had reduced populations to about one-quarter to one-third of historic levels (Bigg 1984, 1985).

Further north in Alaska, control of harbour seals and Steller seal lions began in 1927 to attempt to protect salmon fisheries (Table 2). For almost 50 years, both culls and bounties were employed, but little effort was given to determining by how much the seal populations were reduced. In order to protect coastal fisheries, Oregon also conducted control programs against harbour seals, and both Northern and California sea lions for seven years, beginning in 1925 and again for a period of three decades ending in 1967. These culls were thought to have reduced harbour seal numbers by about 50%. Sea lions declined by an unknown amount.

On the east coast of North America, bounties for harbour seals were begun in the late 1880s in Maine and Massachusetts and about 1927 in Nova Scotia to reduce the number of seals "harassing" and competing with fishermen (Table 2, Boulva 1973). What appears to be the longest control program took place in Massachusetts from 1888-1962. Together with the programs in Maine, it is estimated that between 72,000 and 136,000 seals were killed for the bounty (Lelli et al. 2009). Although the extent of reduction is not known, it was clear that the

populations were greatly reduced. Further north in Nova Scotia, culling did not commence until some 40 years later, but continued for 50 years, ending in 1976. Although aimed at harbour seals, the bounty included an unknown proportion of grey seals until 1949 when the submission of a jaw was required to claim a bounty. This long period of hunting greatly reduced the harbour seal population, although again quantitative estimates of the reduction are not available. In each of the above jurisdictions, there appears to have been no analysis of the benefit of these long-standing culls on fish stocks.

Grey seals had not been part of the initial control program in Nova Scotia, but were included in 1967 and the cull continued until 1983. The bounty on grey seals was extended in 1978 to include the breeding colonies in the Gulf of St. Lawrence and this pup cull continued until 1990 (Table 2). It is clear that these control programs were ineffective at reducing the grey seal population and in fact the population continued to grow (Trzcinski et al. 2006).

On the other side of the Atlantic Ocean, active control programs against grey seals were undertaken in the United Kingdom (reviewed in Bonner 1989; Harwood and Greenwood 1985). In 1934, the south-western Sea-fisheries Board organized the killing of 177 seals, probably grey seals, to protect Atlantic salmon (*Salmo salar*) returning to rivers on the Cornish coast. By the early 1960s, the grey seal population had increased to the point where a Consultative Committee on Grey Seals and Fisheries concluded that although the amount of fish consumption was unknown that the amount must "be scaled in thousands of tons" and that the case against seals was made and control measures should be undertaken. Control in Orkney and the Farne Islands was meant to reduce to the population to three-quarters of its current size by killing moulted pups. The pup cull was conducted annually at Orkney beginning in 1962 and at the Farne Islands (in 1963, 1964 and 1965 only). After 1965, the National Trust, owners of the Island, decided that culling seals was not consistent with the goals of the reserve and did not permit further killing. Despite these short-term culls the populations continued to grow.

Further complaints of damage to fisheries lead to a new control program, which from 1977 to 1982 would have reduced the Orkneys and the Outer Hebrides from the 1976 level of 50,000 to 35,000 by the end of 1982 by killing both adult females and pups. However, public protest after the first cull in 1978 on the Orkneys resulted in a return to pup culling only which had already proved inadequate to limit population increase and had the further undesirable feature that the effects of culling pups were not evident in pup production figures until ~6 years after culling (Harwood and Prime 1978). Several side-effects of the adult female cull were also evident. First, some females failed to return to breed and second, some females that came ashore to breed abandoned their pups when the colony was disturbed (Summers and Harwood 1979). While these unintended effects could be seen as increasing the effectiveness of the cull, they also raise ethical issues in terms of responsible management. Although some culling did occur, there seems to have been no evaluation of the effectiveness of this limited control program on fish stocks.

In Norway grey seals have been hunted along the coast for centuries. In the new management regime there is a provision that in cases of conflicts between seals and fisheries hunting could be used to control seal population size (Nilssen and Haug 2007). Between 1980 and 1990, a culling program was instigated along southern and central coastal areas. Since 2003, in areas of particular conflict with grey seals, Norwegian management authorities have used hunting to control the grey seal population size by permitting a quota of 20-30% of the estimated population size, assessed every five years. A bounty is offered for each documented kill. Although a time series of estimates is not available, there was likely no significant difference in population estimates between those of 1996 to 1998 and those of 2001 to 2003, which suggest

a population of about 4,000-6,000 seals. There seems to have been no evaluation of the effects of controlling seals on fisheries.

Grey seals have also been hunted for centuries at Iceland (Hauksson 2007). The shooting of grey seals is allowed in all areas except the west coast and a bounty program was initiated in 1982 to address conflicts with fisheries. Grey seals, and harbour seals, are thought to compete with cod and to show a preference for cod (Hauksson and Bogason 1997), although the authors of the study provide no evidence for either conclusion other than that cod are eaten by seals. Increased hunting beginning in 1990 resulted in a reduction in the distribution of grey seals and their disappearance along the northeast coast. Abundance estimates indicated that the size of the grey seal population had declined by about 3%/yr between 1982 and 1990 and by 6%/yr from 1990 to 2002 due to the increased hunting effort. The harbour seal population has been reduced by 66%. During this period of culling, cod spawning stock biomass fluctuated without trend and average recruitment declined slightly, suggesting no obvious population response to the seal culls (ICES 2008).

The largest sustained cull of a pinniped occurs in Namibia where since 1993 large numbers of Cape fur seal pups have been killed during the breeding season. The cull began during a period of declining fish stocks thought to be partly caused by poor environmental conditions. Justified to protect fish stocks, the numbers culled have increased from ~50,000 in 1993 to 85,000 in 2009. Each year since 2006, an additional 6,000 adult males have also been culled. There appears to be no published scientific analysis of the predation mortality caused by fur seals or how this mortality compares with other sources of natural mortality on target fish stocks. Again there appears to have been little effort to evaluate the impact of the seal culls on fish stock productivity, although productivity did increase with the return of favourable environmental conditions in the late 1990s (http://www.mfmr.gov.na).

Culls have typically been non-selective in terms of the particular individuals killed. However, recently several selective cull programs have been used to reduce predation mortality caused by seals (Table 2). Cape fur seals prey upon young cape gannets (*Morus capensis*). Between 1993 and 2001 and again in 2007, the targeted removal of fur seals known to have eaten gannets successfully reduced mortality. Selective removal of small numbers of individuals has also being used since 2005 to reduce mortality by Californian sea lions on endangered populations of salmon and steelhead (rainbow trout, *Oncorhynchus mykiss*) on the Columbia River, Oregon.

Cetaceans

Culling of dolphins has an equally long history, having occurred in the Adriatic Sea (Bearzi et al. 2004) and the Black Sea (Mitchell 1975; Birkun 2002) in historical times. Culls were seen as a positive example of fisheries management (Gourret 1894; Del Rosso 1905). The main culling campaign against dolphins, mainly short-beaked common dolphins (*Delphinus delphis*), was launched in 1949 by Croatia with the intent of eradicating dolphins from the Adriatic Sea (Table 2). The Ministry offered rewards for each animal killed, but records on the number of rewards paid could not be found (Bearzi et al. 2004). Bounties to promote dolphin killings were also awarded in Italy from the early 1930s. Although the number of animals killed is poorly documented, dolphin populations are thought to have declined, but the extent of the decline is uncertain.

Dolphins have been viewed as competitors in the yellowtail (*Seriola quinqueradiata*) fishery in Japan since about 1910 when fishermen were paid to kill dolphins (Table 2). Five or so species of dolphins were taken through 1982. As there were no species-specific estimates of the size of

these dolphin populations, it was not possible to determine the impact of culls on either the dolphin species or fishery interactions with any confidence (Kasuya 1985).

Apparently, the only large cetacean to have been culled is the killer whale (*Orcinus orca*) (Table 2). When the Norwegian spring-spawning herring (*Clupea harengus*) population collapsed in the late 1960s, mainly as a result of massive overfishing, the government organized a hunt of resident killer whales which were known to eat herring. Over 700 whales were killed between 1969 and 1980 (Oien 1988). During this period the herring stock remained at very low levels and showed no signs of recovery until the mid 1980s (Dragesund et al. 1997). Killer whale predation does not appear to have been considered further as a limiting factor on herring stock dynamics, although northern minke whale (*Balaenoptera acutorostrata*) predation has been investigated (Tjelmelan and Lindstrøm 2005).

PREDICTING EFFECTS OF PREDATOR REMOVALS ON PREY POPULATIONS AND ECOSYSTEMS

From the previous sections, it is clear that culling marine mammals and other predators has been frequently used in the past as a management tool to attempt to alleviate conflicts. However, less attention has been given to evaluating the success of culls in this respect.

Determining how much larger the yield to a fishery or hunt might be having reduced the predator population is confound by several aspects of predator-prey ecology. Prey species usually have more than one predator and thus gains from culling mammals may be offset by changes in the functional, aggregative or numerical responses of other predators. Predators are rarely dependent on a single prey and this could result in either greater or lesser impact depending on the functional response of the predator. Recruitment to fish populations is highly variable and difficult to predict, but has a large impact on stock abundance. This last point lead participants of the Benguela Ecology Programme Workshop to conclude that comparison of fishery yields before and after a seal cull "would almost certainly not provide a reliable indication of its effect."(Anonymous 1991). Fish usually are the dominate predators in the aquatic ecosystems that have been studied (e.g., Bax 1991; Trites et al. 1997) and so reducing marine mammals would likely produce only marginal increases in yield that could be difficult to detect (Gulland 1987; DeMaster and Sisson 1992).

There have been several attempts to evaluate the benefit to prey populations of culling marine mammals, although these evaluations were generally not part of the control program itself. There are two ways in which the assumption that surplus production from a cull will be available to a fishery can be evaluated: theoretically and empirically (Butterworth et al. 1988) and examples of both are given below.

Despite the long history of non-sustainable harvesting and culling of both harbour seals and Steller sea lions in British Columbia, there has been little analysis of the benefit of this long-term population reduction on the productivity of fish stocks. The large Steller sea lion rookery on the Sea Otter Group off Rivers Inlet was reduced and eradicated during the period 1923-39 mainly to protect the Rivers Inlet sockeye salmon (*Oncorhynchus nerka*) fishery, but there was no discernible change in sockeye catch levels in Rivers Inlet (Peter Olesuik pers comm.), and the sockeye stock has since collapsed (McKinnell et al. 2001). Spalding (1964) compared salmon catches in the vicinity of the Scott Islands, a breeding site for the Steller sea lion, during the late 1950s and early 1960s when sea lions were being reduced, and saw no increase in salmon catches as sea lion numbers declined.

Similarly, only recently have analyses shed some light on the probable impacts of previous harbour seal culling in British Columbia on target prey populations (Peter Olesuik pers comm.). The Strait of Georgia supports the highest density of harbour seals in British Columbia, feeding mainly on Pacific hake (*Meluccius productus*) and Pacific herring (*Clupea pallasii*). Herring stock assessments indicate that herring survival rates have declined as seal predation levels have increased, largely reflecting the increase in the size of the seal population. Selective predation by seals on larger herring within age-classes may also explain an observed decline in the mean weight-at-age of herring as seal populations increased. Stock assessments also indicate the size-at-age of hake declined as seal predation levels increased. In the 1980s, hake in the Strait of Georgia were larger and their diet included fish (mainly juvenile hake and juvenile herring). However, hake now feed on euphausiids and it has been hypothesized that reduced cannibalism by older hake has led to improved recruitment and higher numerical abundance of young hake, which has largely offset the decline in size-at-age. Thus, hake biomass has remained stable. Given this change in diet, it appears that the increase in herring predation by seals has been offset by reduced predation on herring by hake. Consequently, overall predation on herring appears not to have changed much, but seals have displaced hake as the primary herring predator. Recruitment rates of herring have also increased, and there is a positive relationship between seal abundance and herring recruitment (presumably because seals are removing large hake which feed on juvenile herring). Given these interactions, removing seals in the past may have had similar complex consequences on prey population dynamics.

Although the consequences of seal bounties in the Baltic Sea on target fish populations appear not to have been evaluated at the time, the consequences of changes in seals numbers, fishing, and eutrophication in the Baltic over the last century have been recently evaluated using ecosystem models (Hansson et al. 2007). Ecopath with Ecosim software was used to compare different scenarios of seal abundance, fishing pressure, and nutrient loads on fish production, noting that conclusions derived from the model should be used only qualitatively. Status quo scenarios of ~9000 seals were compared with a population of 100,000 seals. Although these figures are substantially below the estimated historical abundances in the Baltic which ranged from ~200,000 ringed seals and 100,000 grey seals (Harding and Harkonen 1999) to upwards of 450,000 ringed seals and 200,000 grey seals (Kokko et al. 1999), they provide a 10-fold contrast. Increasing seal abundance predicted a 30% drop in cod abundance, a lesser decline in herring and an increase in Baltic sprat (*Sprattus sprattus balticus*) abundance. However, if the fishery was managed according to a precautionary approach, the model predicted that seal populations could be as large as a century ago and the stocks of cod and herring would still be as high as or higher than the reference period of 1996-2000. Hansson et al. (2007) summarized the results for over 3400 model runs by stating that "a drastic increase in seals will not necessarily devastate fish stocks." Decrease in benthic production had greater negative effects on cod than an increase in seals.

Predicting the impact of removing predators on prey populations and ecosystems has proven difficult and can lead to unintended consequences (Paine et al. 1998; Scheffer et al. 2001). A good example of this involved studies to understand the interactions between Cape fur seals and hake fisheries in the Benguela Current system off the west coast of South Africa. Two species of hake are involved, one inhabiting shallow-water (*Merluccius capensis*) and the other deep-water (*M. paradoxus*), with the former species predating on small sizes of the deep-water species. Multispecies modelling results show that a reduction of fur seals would likely reduce the abundance of hake since fewer seals would result in more shallow-water hake, a main food of fur seals, and thus more predation on deep-water hake (Punt and Butterworth 1995). A 29-species food web modelling approach of the same seal-hake system (Yodzis 2001) concluded that seal culling may have non-intuitive consequences whereby the removal of an upper-trophic

level predator may lead to increases in another species and that culling was more likely to be detrimental to total yield from all exploited species than it was to be beneficial.

The potential increase in biomass of commercially important fish stocks that might result from a reduction in the number of whales in Northwest Africa and Caribbean ecosystems, where calls for culling have been mounting, has been recently examined (Gerber et al. 2009). The study constructed ecosystem models to account for complex indirect effects of removals on trophic relationships and sensitivity analyses for a wide range of assumptions on whale abundance, fishing mortality and fish biomass. Although as the authors acknowledged the data are often scarce, their results suggested that in the tropical ecosystems, even the complete removal of whales would not lead to an appreciable increase in biomass of commercially exploited fish. By contrast, changes in fishing mortality were predicted to have large positive effects on fish biomass.

Lessard et al. (2005) analyzed two additional predator control case studies to increase a prey species of concern, one aquatic and the other terrestrial. This first case study was the impact of seals on salmon in the Strait of Georgia, British Columbia. Declines of coho (*Oncorhynchus kisutch*) and Chinook (O. *tshawytscha*) salmon appear to have been associated with a decrease in juvenile survival while at sea before returning to the river to spawn. Over roughly the same period, the abundance of harbour seals and California sea lions increased and both species are known to predate on salmon from the stocks that declined. These salmon stocks were expected to benefit from the reduced seal mortality, but compensatory effects of reducing seal abundance were not well understood. Furthermore, as the factor responsible for reducing at-sea survival for juvenile coho salmon was not known, it was not clear if a reduction in harbour seals would reverse the trend. To explore the consequences of harbour seal removal, an ecosystem model was developed using the Ecopath with Ecosim software. The model results showed that reducing the harbour seal population by 90% over a 10-year period had a positive, but only a transient effect during the cull on coho and Chinook abundances. The result was sensitive to the proportion of salmon in the seal diet, which in the case of salmon was considerably uncertain. Further, the result was also dependent on the assumption that Pacific hake, an important predator of salmon did not increase in abundance. However, if hake did increase this could severely increase juvenile salmonid mortality and negate the effect of the harbour seal cull. A lesson from the simulation was that symptomatic control of reducing seals had only transient effects. However, these conclusions have to be taken in the context that they are only model results and are heavily dependent on model assumptions.

The second simulated case study involved two predators – wolves and bears – and two ungulates – caribou and moose (Lessard et al. 2005). The management issue was the alarming decline in caribou populations associated, once again with a decline in juvenile survival and whether the removal of wolves would reverse the decline. In this case, a 10-year pulse of removing wolves hastened an increase in caribou even though controlling moose densities and changing forestry practices provided a more effective long term effect. It was also shown that when combined with moose reduction, a well timed pulse cull of wolves was nearly as beneficial as a sustained cull. However, wolf culling was predicted to have little long-term effect on caribou abundance if moose densities were unchanged. Again, these results underscore the contingent nature of prey response when there are complex multi-species interactions (Lessard et al. 2005).

Another unintended consequence of culling upper-trophic level predators is what has been termed mesopredator release. For example, the removal of coyotes (*Canis latrans*) resulted in increased predation pressure by smaller (meso) body size predators such as foxes, skunks, and cats and the reduction or local extinction of avian prey (e.g., Crooks and Soule 1999). Similarly,

the removal of dingo's (*Canis lupus dingo*) lead to an increase in red fox numbers on the removal side of a dingo exclusion fence in Australia (Letnic and Koch 2010). Culling hooded crows, *Corvus cornix*, appears to have released a larger competitor, the common raven, *Corvus corax*. Ravens ranged more widely, and predation of artificial nests was significantly faster (although total predation was similar), after the removal of crows (Bodey et al. 2009). These and the above examples serve to illustrate that unintended consequences of culling top predators are perhaps not uncommon.

CRITERIA FOR CULLING

In the end the decision to use predator control is a management decision and not a scientific one. This decision should be based on the best available science, but even when the scientific evidence is strong, other factors will influence policy decisions. With respect to predator control in the context of game management, it has been suggested that these other factors would include ethical considerations such as 1) are the goals of predator control acceptable, 2) are the methods of control acceptable, and 3) are the consequences for the target predator and associated non-target species acceptable (Reynolds and Tapper 1996). The second point, acceptable control, raises the issue of the humanness of the method, whereas the third, underscores the need to evaluate the consequence of the control program in a broader ecosystem context.

Culling marine mammals is controversial for four main reasons. The first is that they are regarded as charismatic megafauna and have a high profile in many parts of the world. The second is that many populations of marine mammals are still recovering or have only recently recovered from a long period of over-exploitation and others remain threatened or endangered raising conservation concerns. The third is that the science evidence needed to justify a cull is usually highly uncertain and indirect. This is mostly because of the difficultly in obtaining direct evidence for the negative effects of marine mammal predation on prey populations because predation can rarely be observed and is inferred from estimates of diet. Estimating the diet of marine mammals is fraught with difficulties, not the least of which is obtaining a representative sample of these wide-ranging predators over time and space. The fourth is that those representing the fishing interests often tend to state the evidence for the impact of marine mammal predation on fish stocks as incontrovertible.

There are two fundamental assumptions about culling for the purpose of increasing fish stocks. The first is that marine mammals limit the net production of a fish stock and the second is that any surplus production caused by culling can be used by the fishery (DeMaster and Sisson 1992). Therefore, DeMaster and Sisson (1992) argued that marine mammal control programs should only be considered if the following criteria are satisfied: 1) the magnitude of the increase yield to the fishery can be estimated with its associated uncertainty, 2) the number and age and sex composition of mammals to be removed to maintain the post-treatment level must be specified, and 3) the cost of management must be significantly less than the minimum economic benefit to the fishery.

The United Nations Environment Programme (UNEP 1999), through their Scientific Advisory Committee of the Marine Mammal Action Plan, also considered criteria for culling marine mammals. Based largely on the report of that workshop, the requirements for a cull proposal would include:

1. clearly stated objectives and expected benefits,

2. definition of performance measures that provide a quantitative interpretation of the extent to which objectives have been met and the benefits realized,
3. estimation of per capita seal consumption of target species, the resulting seal predation mortality in relation to other sources of mortality, the size, age structure and duration of the proposed cull, predicted population response of the target population to the cull in an ecosystem context (i.e., accounting for response other strong interactions),
4. sensitivity or robustness of the predicted benefits of the cull to assumptions and uncertainties, and
5. identification of measures used to monitor the target population to evaluate the longer-term consequences of the cull.

Sinclair et al. (1998) attempted to predict the size of the prey population needed to overcome predation effects and the degree of predator reduction needed to allow prey species to increase. The total impact of predation on prey species is a product of the functional and numerical responses of the predator to changes in prey density and to the indirect or trait mediated effects of predators on foraging success and reproduction of prey. In attempting to predict the consequences of the interaction between predator and prey, these authors presumed that predation is known to be the cause of the decline. Sinclair et al. (1998) observed that to counteract predation effects requires knowledge not only of the degree of predation but the nature of the functional response because the stability of the interaction differs depending on the type of functional response. Thus, three types of evidence from a predator-prey interaction are relevant to management and the decision to cull. First, do per capita rates of change increase or decrease with declining prey densities? Second, is predation depensatory or density-dependent, and third, what is the magnitude of predation?

To illustrate the approach, Sinclair et al. (1998) analyzed declining extant populations of marsupials and native rodents in Australia. A plot of the estimated instantaneous rates of increase for the Western barred bandicoot (*Perameles bougainville*) showed those rates declining faster than population size, suggesting depensatory mortality. If predation was the major cause of this mortality, then there would appear to be no stable point in the presence of predation, suggesting a type II functional response. However, there were population sizes over which viable prey populations could exist with a reduction, but not elimination, of predation pressure. Other prey species had stable small populations in the presence of predators, indicating a type III functional response and density-dependent rates of change.

DISCUSSION

Ecologists have known for some time that predators can have significant effects on the structure of terrestrial and aquatic prey assemblages. However, there are few experimental studies of the effects of predation on prey populations in the ocean. The reasons for this are not difficult to appreciate. In place of experiments, several approaches have been used to examine hypotheses about the effects of predators on prey populations. For example, meta-analysis was used to examine the impact of Atlantic cod predation on shrimp (*Pandulus borealis*) populations in the North Atlantic (Worm and Myers 2003).

Culling is widely practiced as a means to limit predation on livestock and game. Historic changes in species' distributions and abundance illustrate that culling programs can be very effective at reducing predator density (Berger 2006), although such substantive impacts are generally considered undesirable for native predators. However, despite their prevalence, the effectiveness, efficiency and the benefit:cost ratio of culling, programs have been poorly studied (Berger 2006; Baker et al. 2008). A survey of studies of lethal control found that 11-71% of

carnivores killed to prevent losses showed no evidence of having been involved in recent conflict (Treves et al. 2004). Berger (2006) evaluated the effectiveness of predator control against coyotes in relation to the sheep production in the United States. Berger found that although the model which best accounted for the trends in sheep numbers over time included predator control, control accounted for only 6% of the trend in sheep numbers whereas economic variables (e.g., unfavourable market conditions) accounted for over 75%.

Lavigne (2003) stated that we should not expect calls for culling marine mammals to abate any time soon. One reason is that there appears to be little correlation between the overall size of a marine mammal population and the conflict they seem to generate with fishermen. For example, although the number remain a small fraction of historic population size, the recovering grey seal population in the Baltic Sea is once again considered a threat and Sweden has issued licenses to shoot several hundred grey seals in response to complaints by fishermen (Västervik 2010). Grey seals were considered pests early in the last century when the population size was small (Scott 1968). Due to their coastal occurrence, grey and harbour seals appear to be considered pests at local to regional scales largely independent of total population size.

The perceived conflict with fisheries has as much to do with fisheries practices and economics as it has to do with the consumption of fish by native marine mammals. Nevertheless, marine mammals are perceived as taking an unfair fraction of those fish left in the water by fishermen. Several authors (Jackson et al. 2001; Lavigne 2003; Roberts 2007) have reminded us that the world's oceans were home to much larger populations of both fish and marine mammals than they are today. Thus, continental shelf ecosystems can simultaneously support large populations of groundfish and marine mammals.

There are several conclusions that can be drawn from experimental studies in terrestrial systems and more model-based approaches in aquatic systems. First, predator removal can increase productivity and population size of target prey populations, but not always. Second, these studies typically have involved large proportional reduction in predator populations, presumably to increase effect size and the statistical power to detect a significant effect. Third, the effects of culling are typically dependent on continued control, and in the absence of control the benefits rapidly disappear. Based on their review of predator control experiments to enhance ungulate densities in North America, NRC concluded that if control where to be used in this way, control must be both intense and frequent and that there is no factual basis for assuming that short-term control will have long-term benefits (Anonymous 1997). Fourth, at least in the case of marine mammals, few studies have clearly articulated measurable objectives for prey population recovery or increase and have evaluated the success of the control program with respect to those objectives. Fifth, culling predators often has non-intuitive and unintended consequences for both target and other predator and prey species.

Lessard et al. (2005) felt that their examples of predator control models served to illustrate that aggressive management controls should not be rejected out of hand. Rather, they should be formally evaluated whereby the potential for unintended negative consequences can be weighed against the risk of no action. However, given that there is often (perhaps usually) as great a deal of uncertainty about the sources and magnitude of mortality on target species, control may result in an increase in the target species or not or may lead to compensatory mortality response from other sources of mortality whereby the effect is reduced.

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Table 1. Approaches to the management of harrier-grouse-hunter conflicts (source Thirgood and Redpath 2008).

Management Zction	Objective	Issue
Financial compensation	Reduce conflict and illegal hunting	Politically , financially and logistically unfeasible
Manipulating habitat	Reduce susceptibility to predation or densities of harriers	Not supported by scientific evidence
Diversionary feeding	Harrier provided with carrion to reduce predation on grouse chicks	No evidence that this leads to increases in grouse densities; also concern that this might increase harrier or other predator densities – again not support by evidence
Harrier density limitation	Encourage recovery of golden eagles (*Aquila chrysaetos*) to prey on harriers	Little evidence this would work, eagles are also killed illegally
Harrier control/removal	Reduce harrier predation by limiting density	Not support by conservationists or UK government

Table 2. Examples of culls conducted to reduce marine mammals to protect fisheries.

Species	Location	Target Prey	Dates	Predator Reduction	Prey Response	Source
Pinnipeds						
Grey and ringed seal	Baltic Sea	Cod, herring, sprat	1889-1927, 1941-1977 Denmark; 1903-1967 Sweden; 1909-1918, 1924-1975 Finland	populations reduced by ~80%	None at time, but recent ecosystem evaluation of scenarios	Harding and Harkonen 1999; Hansson et al. 2007
California sea lion	California	Salmon	~1897-9	unknown	unknown	Merriam 1901
Harbour seal	British Columbia,	Herring, salmon	1914-1963	population reduced 60% from historical level	unknown	Olesiuk 2009
Steller sea lion	British Columbia	Salmon	1913-1916; 1923-1939	local extinction	salmon stock went extinct some time after sea lion exterminated	Bigg 1985; McKinnell et al. 2001; Olesiuk per comm. 2010
Harbour seal and Steller sea lion	Alaska	Salmon in gill net fishery	1927-1967	bounty and cull, not clear how much populations were reduced	unknown	Lensink 1958
Northern and California sea lion;	Oregon	Coastal commercial fishes	1925-1931	Sea lions declined by unknown amount; ~50%	unknown	Pearson and Verts 1970
Harbour seal	Columbia River	Salmon	1924-1933; 1936-1967	reduction in harbour seals		
Harbour seal (mainly)	Eastern USA	Cod, mackerel, other fishes Salmon, lobster	1891-1905; 1937-1945 (Maine); 1888-1962 (Massachusetts)	population was reduced greatly; estimate ~72-136K claimed for bounty	unknown	Lelli and Harris 2006; Lelli et al. 2009

Species	Location	Target Prey	Dates	Predator Reduction	Prey Response	Source
Harbour seal	Nova Scotia	Inshore fisheries	1927-1976	population was substantially reduced	unknown	Boulva and McLaren 1979
Grey seal[1]	Eastern Canada, excluding Sable Island	Inshore fishing gear/catch: cod, salmon, mackerel, herring, lobster	1967- 1983	population continued to increase	unknown	Mansfield and Beck 1977; Zwanenburg et al. 1985
Grey seal	Gulf of St. Lawrence	Not specified	1978-1990	Culling pups - population briefly stabilized	unknown	Lavigueur and Hammill 1993
Grey seal	United Kingdom	Salmon	1934; 1962-1965 – pup culls; 1978 – pups and adult females	Population continued to increase	unknown	Bonner 1989; Harwood and Greenwood 1985
Grey seal	Norway	Coastal fisheries	1980-1990; 2003-	Bounty seems to have stabilized population	unknown	Nilssen and Haug 2007
Grey and harbour seal	Iceland	Cod	1982-	Grey seal reduced by ~33%, harbour seal by 66%	No formal evaluation, cod biomass fluctuated without trend	Hauksson and Bogason 1997; ICES 2008
Cape fur seal	Namibia	Commercial fishes	1993-	Mainly pups killed, population declining	unknown	http://www.mfmr.gov.na
Cape fur seal	South Africa	Cape gannet	1993-2001; 2007	Targetted removal 153 selected individuals	Seal predation mortality ~7%; effects short-term	David et al. 2003; Makhado et al. 2009
California sea lion	Oregon, Columbia River	Salmon	2005-	Selective on few individuals		www.dfw.state.or.us/fish/sealion/index.asp

Species	Location	Target Prey	Dates	Predator Reduction	Prey Response	Source
Cetaceans						
Dolphin sp.	Japan	Yellowtail, damage to gear and catch	~1910-1982	No evaluation of success of culling; unknown effects on dolphin numbers	no evidence that cull had any positive impact on yellowtail	Kasuya 1985
Short-beaked common dolphin *Delphinus delphis*; some bottlenose dolphin	Adriatic Sea	Fisheries in general	Historical times; 1940-1960 (Croatia); 1930-1960s (Italy)	Dolphin populations declined by unknown amount	no evaluation of effects on fisheries	Bearzi et al. 2004
Killer whale	Norway	herring	1969-1980	700 whales	Stock failed to recover until mid 1980s	Øien 1988; Dragesund et al. 1997